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Canopy Dieback in a New Zealand Mountain Beech Forest[1]

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ABSTRACT: Accelerated mortality is attributed to an unusually high percentage of old trees, an abundance of pathogenic fungi, and a putative lowering of water tables in the 1960s. There is some evidence to suggest that this may be a cyclical phenomenon.

Mountain beech (*Nothofagus solandri* var. *cliffortioides*) is one of two varieties of a widespread indigenous New Zealand tree. Particularly associated with mountain regions, it is found over a wide range of generally poor soils and is often the forest of the timberline. The present study was undertaken on the northwest slopes of Mt. Ruapehu (39°16′ S, 175°35′ E), Tongariro National Park, where mountain beech mortality appears to be high over substantial areas. The degenerate appearance of the forest, with large numbers of dead trunks and intertwining masses of silvery leafless lichen-covered branches, was not in evidence prior to 1967, according to reliable local opinion and as seen in aerial photographs. With a view to explaining this situation, investigations were undertaken in 1973.

General Biology

As a result of detailed inquiries by Wardle (1970*a*, *b*, *c*, *d*, 1974), the general biology and ecological performance of mountain beech are well documented. In the context of accelerated mortality, however, some features can appropriately be emphasized. Flowering is an irregular phenomenon, and even when profuse is not necessarily followed by prolific seeding. Indications are that from the point of view of production of an abundance of viable seed, good years occur about once in a decade, with perhaps two or three minor mast years in between.

Seedfall occurs in late summer or autumn, and germination takes place the following spring. Seeds are dispersed by wind and are rarely thrown more than a few meters from the tree on which they originate. The chances of germination and early survival seem much greater if the seed should fall in beech litter. Although seedlings soon become capable of an annual increase in stem length of 30–40 cm, the usual situation in a forest with a closed canopy is for seedlings to enter a semidormant state during which height increase may be little more than 1 cm/yr. A mountain beech plant in a forest may therefore be less than 50 cm in height yet more than 20 yr old. Such a plant is of shrublike form and at an advanced growth stage. This semidormancy can be broken only by the advent of high light intensity, which usually occurs upon the death of canopy trees. Rapid growth characterized by strong apical dominance follows, as poles are produced. Ultimately, a single survivor will spatially replace the tree whose death 100 or more years previously allowed light to break the dormancy of perhaps dozens of young plants near the forest floor.

Stands are often of even age, and trees therefore tend to reach the fragility of old age more or less simultaneously. A severe environmental stress such as a storm or heavy snowfall may therefore kill a large percentage of trees in an aging stand. Normally, these would be replaced from the crop of young plants on the forest floor. Thus, once established, the phenomenon of even-aged stands tends to be self-perpetuating.

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TABLE 1

GENERAL SITE DESCRIPTION

SITE	ALTITUDE (m)	ASPECT	SLOPE	GENERAL
1	1,320	NW	10°	Damage light
2	1,240	NE	40°	Near ridge top; steep
3	1,210	SW	8°	Shady
4	1,120	NW	2°	In continuous bush; widely representative
5	1,070	NW	1°	Isolated copse
6	1,060	N	5°	On stream bank
7	1,030	W	2°	In continuous bush
8	890	—	Flat	Part of large isolated stand

Boring insects, particularly adults and larvae of the indigenous coleopteran *Platypus* are known to attack dead and stressed trees (Miller 1971). In the presence of an excessive amount of dead wood, Milligan (1972) has demonstrated that they will attack living trees of *Nothofagus fusca*. A variety of fungal pathogens are associated with beetle tunnels (Faulds 1973); *Armillaria* is particularly implicated, and Milligan (1974) has described *Platypus* feeding on yeasts in the tunnel linings.

METHODS

Trees from eight sites, chosen to encompass a range of altitude and aspect and to include both severely damaged and relatively unaffected stands (Table 1), were examined. Measurements involved diameter at breast height of all trees over 2 m tall in each sample. At sites 2, 4, and 8, trees were sampled by point quarter with centers along arbitrary lines. At each of the other sites, all trees in variously circumscribed quadrats were evaluated.

All trees in a 50-m-square quadrat were measured at site 1. There were 136 in total, including 8 recently dead but still standing. As the histogram for site 1 in Figure 1 reveals, there was generally an increase in the number of trees in successively smaller classes, although there were fewer than might be expected in the 25–30-cm class. There was no sign of small beech seedlings, although some advanced-growth plants were present.

Size distribution was similar at site 2, where 200 trees were sampled. There was a higher number of seedlings than at any other site, and most of them were at the advanced-growth stage.

At site 3, trees seemed to be younger. Of 182 only 3 were over 30 cm and none were over 40 cm. There were relatively few in the two smallest size classes. It seemed that mortality had occurred at all ages. In fact, in each of the three classes represented by more than 35 trees, the proportion dead was very similar (40.7%, 41.3%, and 35.1%). Relative to most other sites, seedlings were abundant.

More trees might have been expected in the three smaller size classes at site 4, where 252 trees were sampled, 87 of which comprised a standing dead subsample. Mortality was not evident in the smaller classes, although both subsamples revealed a dip in the histogram in the 35–40-cm class. Seedlings, particularly young ones, were quite well represented.

More than half of the 185 trees at site 5 were dead though still standing, and in both subsamples there was a suggestion of paucity among smaller classes and in the 25–30-cm class. There were very few seedlings.

Site 6 was another at which there were virtually no larger trees. Of the 274 trees measured, 57 were dead, and mortality seemed spread throughout the size classes. No small seedlings were noted, although there were some young plants at the shrub stage.

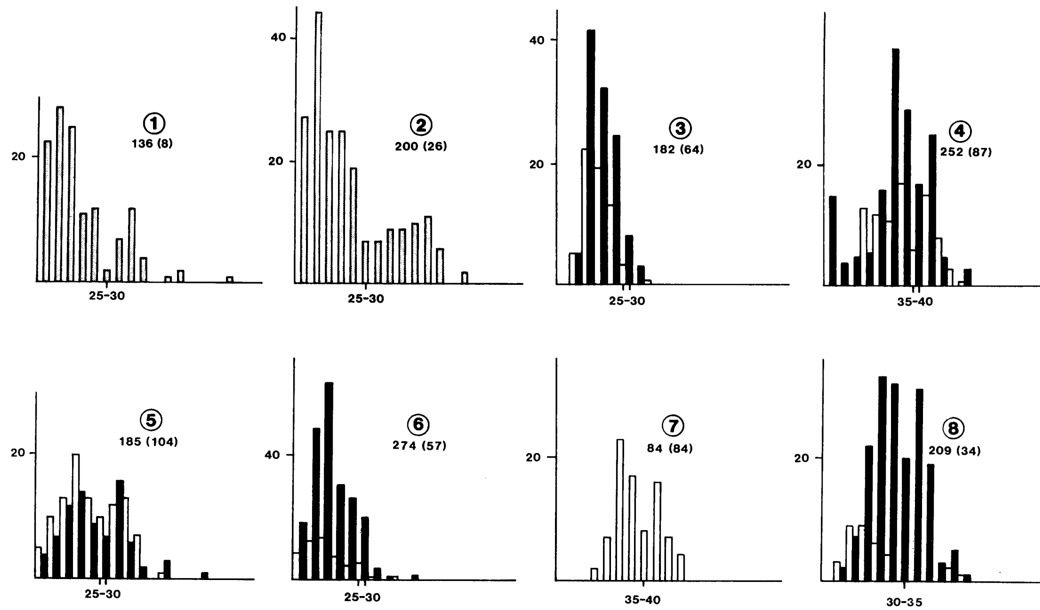

FIGURE 1. Histograms showing size class distribution at each of eight sites. Vertical axes = number of trees; horizontal axes = size classes (5-cm-diameter at breast height intervals); solid blocks = living trees; open blocks = standing dead trees; stippled blocks = total living and standing dead trees (sites 1 and 2); total number of trees at each site is given below each site number, with number of standing dead trees given in parentheses.

All 84 trees were dead at site 7, where again there were no trees in the smaller classes and an evident scarcity in a medium-sized group (30–35 cm). More trees than at any other site fell into the larger size classes (over 30% were in excess of 40 cm). There was no sign of any individual less than 15 cm.

At site 8, 209 trees were measured. Once more there seemed a partial lack of trees both in the smallest classes and that embracing 30–35 cm. The majority of the dead trees were small. Some seedlings were present.

No attempt was made in the field to collect information pertaining to the physical environment. Records for precipitation at Chateau Tongariro (within 10 km of each site) are complete from 1937. Available information to 1972 provides an annual mean of 2481 mm. Rainfall had evidently been less toward the end of the period: in 1968–1972, the average annual mean was 8.8% lower than in the previous 25 yr, and summer rainfall was 8% lower during 1960–1969 than during 1940–1959.

DISCUSSION

The numbers of trees in the smaller size classes, and by inference younger age classes, are low or even nonexistent. In a forest type where even-aged stands are not atypical, this is no real surprise although it does suggest that recruitment had been low for some decades prior to the 1960s. It also implies that over this period the forest had been an aging one with light mortality, but mortality must have greatly accelerated by 1970.

Even when trees from two atypical healthy sites are included, 464 (30.4%) of the total standing trees evaluated (1522) were dead and perhaps a further 10% were dying. Although dead trees doubtless remain standing for several years, the value is greatly in excess of the general figure of 3% per year determined by Wardle (1970*d*). It also seems fair comment that the forest investigated was old, certainly in relation to "mixed-age" stands described by Wardle (1970*d*). Over 70% of trees in his stands were less than 6.5 in.

(approx. 16.6 cm) in diameter. In the present study, only 37% were less than 15 cm in diameter. Similarly, less than 6% of Wardle's trees were over 15.5 in. (31 cm); in this assessment, nearly 30% were over 30 cm.

Assuming the forest is generally old, it would not be surprising if its trees were vulnerable in the presence of any factor or factors that induce particular stress. It is suggested that the stress leading to accelerated mortality in this case took the form of lowered water tables, consequent on the reduced precipitation levels of the 1960s. Admittedly, trees tend to be dying in all size classes (Figure 1), yet it has been shown by Atkinson and Greenwood (1972) albeit in a rather different type of New Zealand forest, that drought is a stress agent and may adversely affect trees of all sizes. Furthermore, it may be that the situation has been exacerbated by boring beetles attacking living trees. Such an event may not be usual but has been shown by Milligan (1974) to be possible. In the course of the present investigation some beetle holes were noted in seemingly healthy trees, although the information was not quantified.

The data suggest that at most sites the forest could be described as "two-aged," a situation evidently regarded as not uncommon by Wardle (1970*d*).

At all sites apart from the two at which larger trees were lacking and in all subsamples, there was a partial absence of trees in one or other of the medium-size categories. This suggests a period of low recruitment at some time in the past. Precisely when is not easy to say. It could vary from site to site, although the classes do tend to be among smaller trees at the higher (and colder) sites and larger ones at lower (and warmer) sites. Since diameter growth is reported to be significantly slower at higher altitudes (Wardle 1970*d*), the period could be more nearly contemporaneous between sites than the raw data suggest. In my investigation, only occasional attempts were made to age trees, but these, plus extrapolation from the much more extensive data presented by Wardle (1970*d*), suggest that the period of this regeneration gap would have been at least 100 yr previously. Following that phase there appears at each site to have been a rise in recruitment rate. When this occurred is similarly unclear, but even a minimum value would predate reliable ecological writings. However, in a report on Tongariro National Park, Cockayne (1908) stated, with special reference to mountain beech, that "dead trees still standing and prone are a feature," and that "seedlings and saplings are in abundance." A photograph supports the former comment. One should not, of course, expect an "abundance" of saplings unless there had been a recent increase in light on the forest floor, an event that would logically follow accelerated death of canopy trees. Neither should one expect dead trees to be a "feature." Surely, neither comment could be construed as applying to an average mountain beech forest. The possibility then arises that Cockayne's survey was undertaken during a period of widespread regeneration following excessive tree mortality. It is, in turn, possible that the regeneration gap suggested by the absence of medium-sized trees in the present survey was a consequence of a period of low recruitment that preceded the period of excessive mortality. The implication is that about 100 yr ago the mountain beech forests in the locality were exhibiting dieback. Perhaps a cyclical phenomenon is involved.

The key to the short-term future of these forests lies in the seedlings and the survivors. Where mortality is total and there are no seedlings, as at site 7, there can only be gradual reestablishment over scores of years as the slow migration typical of beech occurs from the periphery of the devastated area. There are other similar situations in the locality, but they do not appear to be widespread. Most of the forest is typified by the other sites where seedlings and young plants do exist. Without meticulous counts it is difficult to place a value on their density, but my subjective estimation would be that it exceeds the minimum believed by Ogden (1971) to be necessary to maintain a red beech forest. Decimated though this mountain beech may at present appear it can generally be expected to reestablish itself as a forest within the next 20 yr.

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